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SHORT REPORT

Mate guarding in the Linnet *Carduelis cannabina*

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In monogamous bird species, females frequently engage in extra-pair copulations (EPCs) which often result in extra-pair fertilisations (EPFs).[1] To ensure paternity, males therefore often guard their mate during the female fertile period, which enables the pair male to interfere successfully with intruding extra-pair males.[2,3] Frequent within-pair copulations are also commonly used as a paternity guard in monogamous birds.[1] Mate guarding and frequent copulation tend to be alternative strategies for paternity assurance.[4]

In the Linnet *Carduelis cannabina*, a socially monogamous passerine, males use frequent within-pair copulations as a paternity guard during their mate's fertile period.[5] However, as we show in this paper, male Linnets also have extensive mate guarding behaviour. After documenting and quantifying this behaviour, we discuss the cost of mate guarding and the advantages of using both frequent copulations and mate guarding for paternity assurance.

The study was performed in Denmark during the summers of 1994 and 1995 in a plantation of young Caucasian Firs *Abies nordmanniana*, where the breeding population of Linnets was estimated to be 40–50 pairs in both years. Behavioural observations were conducted between 06:00 and 12:00 hours from late April to mid-July, and consisted of 30-min focal watches of individual pairs. Focal individuals were chosen among birds in any stage of breeding, from nest-site selection to incubation. Observations of a focal pair were conducted daily until the female commenced incubation. During the incubation period, observations were made less frequently. The carotenoid pigmentation displayed on the breast and crown of male Linnets was highly variable among individual males, both in intensity and pattern, which allowed easy recognition of the focal males. Focal females could not be identified on their plumage coloration, but could easily be identified by their behaviour, because only the pair-females were engaged in nest building and incubation. Focal females could therefore be identified correctly, since the pair-female usually visited the nest whenever she arrived near the nest-site, and because she was followed closely by the guarding pair-male.

During each focal watch, the distance between pair members was estimated by eye to the nearest metre at one-minute intervals, while movement initiations and intrusions were recorded continuously during the focal watches. A move was defined as any flight of 10 m or further away from the other pair member. Which sex initiated the move and whether the move was followed by the other pair member within the next 10 s were recorded. An intruder was defined as any bird that appeared without a mate within 5 m of one of the focal pair members. The sex of the intruder was recorded, along with the pair members' reaction towards the intruder (either a chase response, or no response towards the intruder).

The intensity of mate guarding was calculated as the percentage of time the male spent within 10 m of the female. A distance of 10 m between the pair members seemed to be sufficiently close for focal males to prevent other males from attempting EPCs with their female, since the open habitat of the young coniferous trees facilitated the discovery of approaching males.

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To standardize the timing of the fertile period of females, the laying day of the first egg was designated as day 0. During data analysis, the nesting cycles of the females were divided into three periods according to the time of ovulation: the pre-ovulatory period (up to and including day –2), the ovulation period (days –1 to +3), and the post-ovulatory period (from day +4 onwards). Females laid one egg each day during the laying period and the mean (± se) clutch size was 5.0 ± 0.1 (n = 47). The ovulation period was therefore defined from day –1 to +3, because the first egg is ovulated the day before it is laid.

Males spent 95–100 % of their time within 10 m of their females from eight days before egg-laying until the onset of laying (Fig. 1). However, whether this intensive mate guarding was initiated at the time of pair formation is unknown, since the breeding pairs could only be followed from the onset of nest building.[5] When the first egg was laid, mate guarding intensity started to drop and declined significantly during the laying period (Pearson correlation: r = –0.99, n = 5, P < 0.001) to a mean (± se) intensity of 18 ± 5 % (n = 7 males) in the post-ovulatory period.

Throughout the nesting cycle, males always responded immediately to female-initiated moves by following the female closely. Table 1 shows the frequency of movements initiated per pair and the proportion of these moves initiated by the female during the three periods of the nesting cycle. There was a significant decline in the proportion of moves initiated by the female from 93% in the pre-ovulatory period to only 19% in the post-ovulatory period (Friedman test: χ^2 = 14.11, df = 2, n = 9 pairs in each period, P < 0.001). Thus, since female-initiated moves were always followed by the male, it was the male that was responsible for maintaining pair proximity during the fertile period of the female.

Table 1. The number of moves initiated by pair-members per h and the percentage of these moves initiated by the female in the three periods of the nesting cycle. Values are means (± se) for nine focal pairs.

Period	Total moves per h	Female initiated moves (%)
Pre-ovulatory	3.7 ± 0.6	93 ± 3
Ovulatory	1.5 ± 0.2	68 ± 12
Post-ovulatory	0.7 ± 0.3	19 ± 10

The Linnets did not defend territories during the breeding season, but both males and females were observed defending mates against intruders. Out of 78 intrusions observed during the focal watches, 47 were male intruders, two were females and 29 were of unknown sex. Of these, 85% were chased away by the pair-male, while only 3% were chased away by the pair-female. In the rest of the cases neither of the pair members reacted to the presence of the intruder. The mean (± se)

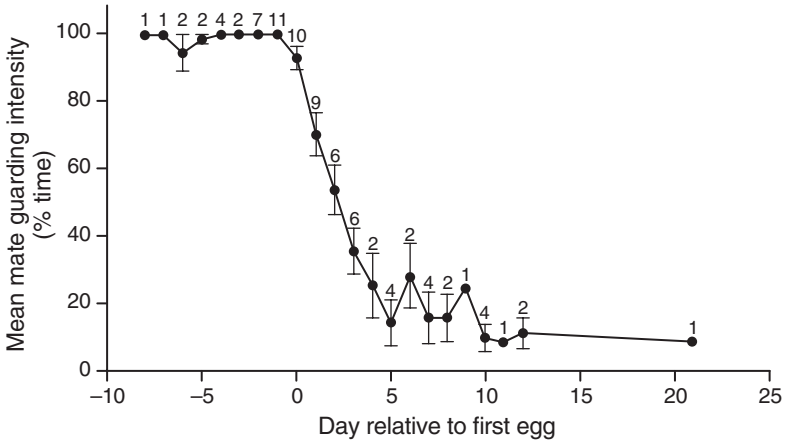

Figure 1. Mean (± se) intensity of mate guarding in relation to the nesting cycle of the female. Values are the percentage of time spent within 10 m of the female. Day 0 = day of first egg. Numbers above the points give the number of focal pairs observed on a given day.

frequency of intrusions were 0.24 ± 0.08, 0.28 ± 0.06 and 0.03 ± 0.03 intruders per h for the pre-ovulatory, the ovulation and the post-ovulatory periods, respectively. There was a significant decline in intruder frequency in the post-ovulatory period (Friedman test: $\chi^2 = 6.81$, df = 2, $n = 9$ pairs in each period, $P = 0.03$), but no significant difference was found in the number of intruders in the pre-ovulatory and the ovulation period (Wilcoxon paired-sample test, $n = 9$, $P > 0.50$).

The data presented here show that, in addition to frequent within-pair copulations,[5] Linnets also use mate guarding as paternity guard. The way in which the intensity of mate guarding varied with respect to the female cycle was similar to that found in other studies of mate guarding passerines,[3, 6–8] with a peak in intensity during the pre-laying period and a decline during the laying period. Compared to these other studies, male Linnets seem to be among the more intensively guarding passerines, with the male spending 95–100 % of his time within 10 m of the female from eight days before egg-laying. In general, intense mate guarding may incur increased energy expenditure, reduced foraging opportunities, increased risk of injury and reduced opportunities for EPCs for males.[1] However, the very intense mate guarding in Linnets did not seem to incur considerable costs. The energy demands seemed to be low, since guarding males spent much of their time perched, seemingly waiting and watching over the female. Being granivorous,[9] males had plenty of opportunity for foraging when they followed their females during her collection of nesting material on the ground. The chasing of intruders rarely resulted in fights between the pair-male and intruder. The few fights observed were not intense, and no cases of predation of guarding males were observed during 295 hours of focal observation, so that risk of injury due to mate guarding was probably low. Lost chances of engaging in EPCs due to the intense mate guarding would also be relatively low, since males had plenty of opportunity for such behaviour following the termination of their mate guarding, due to the asynchronous breeding of the Linnets within the study area.[5] Thus, the overall costs associated with the very intense mate guarding in Linnets does not at least seem to be high.

The combined use of both mate guarding and frequent copulations as paternity guards is unusual in birds, since these two types of paternity guards are normally regarded as alternative strategies for paternity assurance.[4] The reason why male Linnets use both types of paternity guards may be that they generally experience a high risk of EPC attempts (see below), and that neither mate guarding nor frequent copulations are excessively costly.

The semi-colonial breeding and multiple asynchronous broods in the Linnet [5,9] provide ample opportunities for EPCs.[1,10] No EPC attempts were observed, however, in the study population,[5] although all intrusions occurred in the pre-ovulatory and the ovulation period, indicating that extra-pair males tried to time their intrusions in accordance with the fertile period of females. Recent molecular evidence has shown that EPFs did occur in the broods of Linnets sampled in a neighbouring population in 1998 (J.B. Pedersen, unpubl. data). Thus, even with the use of two simultaneous paternity guards, Linnet males were not able to defend their paternity with 100% efficiency.

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REFERENCES

1. Birkhead, T.R. & Møller, A.P. (1992) *Sperm competition in Birds: Evolutionary Causes and Consequences*. Academic Press, London.
2. Beecher, M.D. & Beecher, I.M. (1979) Sociobiology of bank swallows: reproductive strategy of the male. *Science*, **205,** 1282–1285.
3. Birkhead, T.R. (1979) Mate guarding in the magpie *Pica pica*. *Anim. Behav.*, **27,** 866–874.
4. Møller, A.P. & Birkhead, T.R. (1991) Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour*, **118,** 170–186.
5. Drachmann, J., Komdeur, J. & Boomsma J.J. (1997) Copulation behaviour in the Linnet *Carduelis cannabina* and the insemination window hypothesis. *J. Avian Biol.*, **28,** 191–196.
6. Carlson, A., Hillström, L. & Moreno, J. (1985) Mate guarding in the Wheatear *Oenanthe oenanthe*. *Ornis Scand.*, **16,** 113–120.

7. Møller, A.P. (1987) Extent and duration of mate guarding in Swallows *Hirundo rustica*. *Ornis Scand*., **18,** 95–100.
8. Sheldon, B.C. (1994) Timing and use of paternity guards by male chaffinches. *Behaviour,* **129,** 79–97.
9. Newton, I. (1972) *Finches*. Collins, London.
10. Møller, A.P. & Birkhead, T.R. (1993) Cuckoldry and sociality: a comparative study of birds. *Am. Nat*., **142,** 118–140.

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